

# Ravens, *Corvus corax*, follow gaze direction of humans around obstacles

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The ability to follow gaze (i.e. head and eye direction) has recently been shown for social mammals, particularly primates. In most studies, individuals could use gaze direction as a behavioural cue without understanding that the view of others may be different from their own. Here, we show that hand-raised ravens not only visually co-orient with the look-ups of a human experimenter but also reposition themselves to follow the experimenter's gaze around a visual barrier. Birds were capable of visual co-orientation already as fledglings but consistently tracked gaze direction behind obstacles not before six months of age. These results raise the possibility that sub-adult and adult ravens can project a line of sight for the other person into the distance. To what extent ravens may attribute mental significance to the visual behaviour of others is discussed.

**Keywords:** raven; *Corvus corax*; gaze following; visual perspective taking

## 1. INTRODUCTION

One of the benefits of social life is gaining information from conspecifics, including determining the location of food or predators (see review in Giraldeau 1997). One source of information is in the direction of the other's gaze (i.e. head and eye direction (Byrne & Whiten 1988; Tomasello & Call 1997)). The ability to follow gaze direction has recently been shown for a number of primates (see review in Emery 2000) and other social mammals such as dogs, *Canis familiaris* (Miklósi *et al.* 1998), dolphins, *Tursiops truncatus* (Tschudin *et al.* 2001), and goats, *Capra hircus* (Kaminski *et al.* 2001). Studies follow different paradigms that require individuals either: (i) to visually co-orient with a conspecific and/or human experimenter for tracking locations above, behind or to the side of them (e.g. Itakura 1996; Povinelli & Eddy 1996a, 1997; Emery *et al.* 1997; Tomasello *et al.* 1998); or (ii) to use gaze direction of informed models for locating hidden food (i.e. to select a baited container out of a set of several containers (e.g. Anderson *et al.* 1995; Call *et al.* 1998; Itakura & Tanaka 1998)). Related studies require individuals: (iii) to use the visual attention of others to beg for food and/or assistance from human experimenters (e.g. Call & Tomasello 1994; Povinelli & Eddy 1996b,c); or (iv) to selectively retrieve food from conspecific competitors (Hare *et al.* 2000, 2001, 2003).

At the comparative level, species differ in the extent to which and the context under which they can use gaze information (Anderson & Mitchell 1999; Agnetta *et al.* 2000; Call *et al.* 2000). For instance, species may perform better in a competitive or cooperative task (Hare *et al.* 2002); some appear to rely on a combination of eye gaze and head orientation; whereas others may (learn to) respond to eye gaze alone (e.g. Povinelli & Eddy 1997; Vick & Anderson 2000; Gallese *et al.* 2002). These

differences may be a result of methodological constraints (e.g. salience of task in evolutionary terms (Hare & Wrangham 2002)) but may also reflect different cognitive processes. It has been suggested that the understanding of visual perception of others may take different forms (Byrne & Whiten 1992; Whiten 1996), from the use of gaze as a behavioural cue to the understanding that the visual experience of others is analogous to one's own visual experience (Povinelli & Eddy 1996a; Tomasello *et al.* 1999; see also Povinelli *et al.* 2000; Hare *et al.* 2001).

In contrast to the work on mammals, little is known about gaze following in birds. Sparrows, *Passer domesticus*, respond to different orientations of a human face with different intensities of fear behaviour (Hampton 1994) and ground-nesting plovers, *Charadrius* sp., adjust their injury-feigning displays in response to the gaze direction of human intruders (Ristau 1991). Bee-eaters, *Merops orientalis*, entering their nest holes even appear to distinguish whether or not the view of a human predator is obstructed by natural barriers (Watwe *et al.* 2002). Joint attention with humans, however, positively affects vocal learning in tame grey parrots, *Psittacus erithacus* (Pepperberg & McLaughlin 1996). Despite these promising findings and although birds are visually based animals, standardized tests on gaze following have not been conducted, possibly because the large peripheral field of vision in birds makes it difficult to determine where an individual is looking (Emery & Clayton 2004; but see Zeigler & Bischof 1993; Dawkins 2002). However, such problems also apply to studies on mammals with laterally placed eyes (McKinley & Sambrook 2000; Kaminski *et al.* 2001).

Ravens are scavengers that frequently compete with conspecifics (Heinrich & Marzluff 1991; Marzluff & Heinrich 1991) and potential predators (Bugnyar & Kotrschal 2002a; Stahler *et al.* 2002) over food. During crowd foraging, individuals use a variety of tactics to keep food safe from conspecifics (Heinrich & Pepper 1998; Bugnyar & Kotrschal 2002a) and thereby, like scrub jays, *Aphelocoma californica* (Emery & Clayton 2001), may employ cognitively demanding skills. For instance, caching individuals

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hide from potential thieves (Bugnyar & Kotrschal 2002b). Because visual attention towards competitors may be an important component of such tactical manoeuvres, we predicted that ravens would be able to follow the gaze direction of others.

To distinguish between the possibilities that visual co-orientation may result from some kind of mental experience (e.g. a representation of seeing as mental state) or merely from a combination of orientation responses (e.g. a tendency to look in the direction that others are looking until something of interest is detected), we tested ravens not only for the ability to follow a human's gaze above them but also to a specific location behind an opaque barrier. The former 'high-level' cognitive model predicts that ravens should be able to follow the gaze geometrically around the barrier because they would be capable of understanding that others can see things that they cannot see. The latter 'low-level' cognitive model predicts that the birds' attention should be caught at the barrier because individuals would simply follow a vector away from the other's face and search along this path until something of interest is found and, if nothing 'novel' is present, stop searching. To date, the barrier-test has been performed, to our knowledge, only with chimpanzees, *Pan troglodytes* (Povinelli & Eddy 1996a; Tomasello *et al.* 1999). Human infants solve similar tasks at *ca.* 18 months of age (Butterworth & Jarrett 1991).

Because cognitive processes that accompany gaze following emerge successively in human children (e.g. Butterworth & Jarrett 1991; Corkum & Moore 1995) and, to some extent, also in primates (Tomasello *et al.* 2001; Gallese *et al.* 2002; Okamoto *et al.* 2002), we tested juvenile ravens at two months of age when they were still dependent on the care of their (foster-) parents and again at six months of age when they were totally independent. In addition, we compared the behaviour of those young birds with that of an adult.

## 2. METHODS

### (a) Subjects

We used seven hand-raised ravens (five males, two females), all of which had been tested in previous studies on food caching. Six out of the seven birds were juveniles in their first year; one bird was in its fourth year. All birds were marked with collared rings for individual identification. They were housed together in a *ca.* 725 m<sup>3</sup> outdoor aviary complex composed of three sections. Testing took place in the experimental room (4.5 m × 5 m × 3 m) of section C (figure 1). This room is visually isolated from the rest of the aviary by a solid wooden wall (front wall; 4.5 m × 3 m) and in the middle partly divided by another solid wooden wall (barrier; 1.7 m × 2 m) that is perpendicular to the front wall (figure 2). Birds were fully habituated to the experimental set-up and did not show any interest in the barrier and its immediate surrounding outside of testing. Subjects were fed on their normal diet and normal schedule during testing.

### (b) Apparatus and procedure

Subjects were tested individually by a human experimenter (E). Because the visual behaviour of birds consists mainly of head and eye movements (Dawkins 2002), all look-cues involved a change of E's head angle plus eye direction. In look-around trials, E looked towards the sky. In control trials, E looked

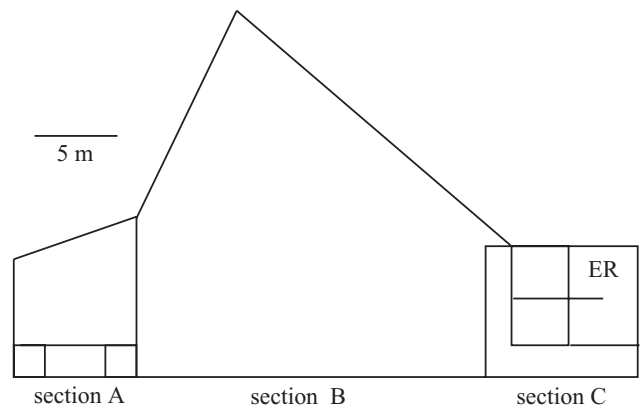


Figure 1. Sketch of aviary complex, indicating the position of the experimental room (ER) in section C. Sections A and B contain the roost and main keeping compartments.

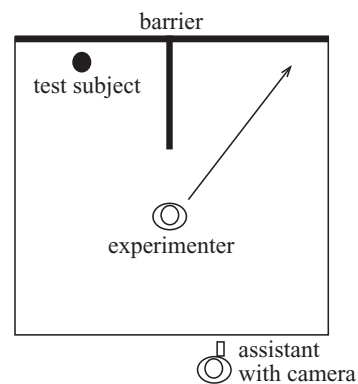


Figure 2. Layout of the barrier situation, showing the position of the human E and the start position of the test subject. The arrow indicates where E looked in the test condition (the control was to the opposite side of the room).

in the direction of the bird (but not directly at the bird). For testing the ravens' tendency to follow E's gaze around the barrier, E waited until the bird was on the ground beside the front wall (either left or right from the barrier). In look-around trials, E looked towards the corner that was behind the wooden barrier and thus outside the view of the test subject (figure 2). In control trials, E looked in the opposite direction (i.e. on the side of the test subject (Tomasello *et al.* 1999)). Subjects were not rewarded in any way for any particular response. Each bird received a total of five sessions, each of which consisted of all four trials. The order of experimental and control trials was counterbalanced within subjects per daily session. To minimize habituation, sessions were conducted within a 15-day period.

Two humans who were familiar with the birds served as E in a randomized order. E was together with the test subject in the experimental room, kneeling 1 m in front of the barrier (figure 2). The second person videotaped the bird from outside the aviary (*ca.* 3 m distance to barrier). E began a trial when the subject was positioned appropriately and was looking towards E. E vocally indicated the onset of a cue but not what type of cue for later video-analysis. To give the cue, E moved his head and eyes in the appropriate direction for 5 s. After giving the cue, E waited at least 30 s before continuing with the next trial. The response of the test subject was measured for 10 s following each cue presentation. In the first test series with two-month-old birds, one juvenile hesitated to land on the ground of the

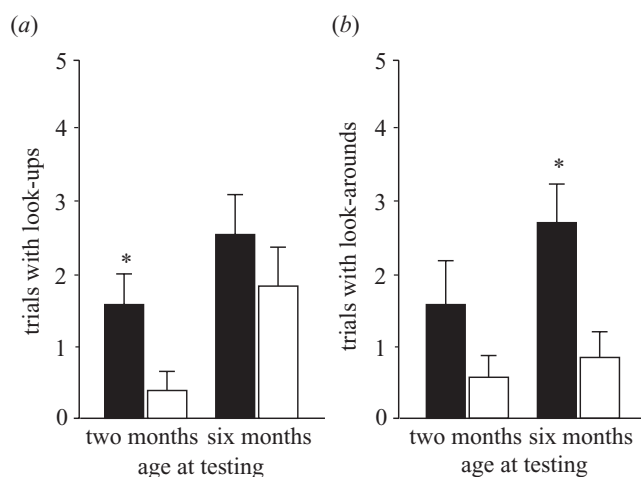


Figure 3. Effect of experimenter's gaze on the visual behaviour of ravens at two and six months post-fledging. Mean (+ s.e.) number of trials in which birds (a) looked up after cue presentation (filled bars) and in the control (open bars) and (b) looked around the barrier after cue presentation (filled bars) and in the control (open bars). Exact Wilcoxon signed-ranks test. Asterisk denotes  $p < 0.05$ .

experimental room and thus could not be tested for looking around the barrier.

### (c) Analysis

All trials were scored from videotapes independently by both experimenters. Paying explicit attention to the visual behaviour of birds (Zeigler & Bischof 1993), we used head orientation (beak lateral or horizontal) and head movement (e.g. switching from right to left eye up) as criteria for looking (Dawkins 2002). In the barrier test, discrete locomotion patterns (walking towards, around, or flying on top of the barrier) emphasize the birds' responses. Experimenters had an agreement score of 98% out of the total of 250 trials. To assess the reliability of categories, we tested eight control observers, who had only limited prior knowledge of raven behaviour, with a randomly assembled sample of 10 trials. After watching a tutor tape with a commentary on the different parameters, observers correctly coded 94% of the trials. We used Wilcoxon signed-ranks test for all statistical comparisons. Owing to our small sample size, we calculated the exact  $p$ -values using table J in Siegel & Castellan (1988). Alpha was set at 0.05.

## 3. RESULTS

On average, ravens used the experimenter's gaze to track locations above them (figure 3a) as well as behind the barrier (figure 3b) in about one-third and half of the cases, respectively. By following look-ups, birds moved their heads laterally with one, predominantly the left, eye directed upwards for a mean ( $\pm$  s.e.) duration of  $3 \pm 0.4$  s. For tracking the gaze behind a barrier, birds repositioned themselves in such a way that they could see where the experimenter was looking, i.e. they walked around or flew on top of the barrier, and gazed in the indicated direction, alternating between the eyes  $2 \pm 0.2$  times (with no clear tendency to use one eye more often). However, birds did not meet the criteria for look-around when they tracked

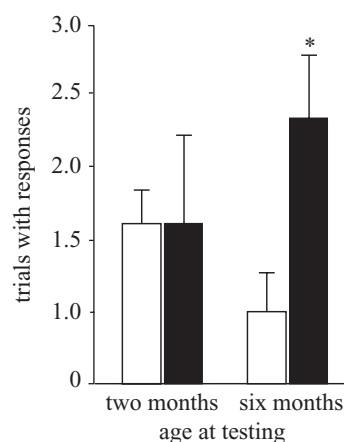


Figure 4. Mean (+ s.e.) number of trials in which two-month-old and six-month-old birds followed E's looks towards (open bars) and behind (filled bars) the barrier. Exact Wilcoxon signed-ranks test. Asterisk denotes  $p < 0.05$ .

the experimenter's gaze to the barrier and searched in front rather than behind it (figure 4).

Both types of gaze following differed between the two time periods of testing (figure 3a,b; table 1). Two-month-old birds significantly followed the experimenter's look-ups ( $n = 6$ ,  $c_u = 53$  and  $p = 0.013$ ), but the effect was not significant when birds were six months of age ( $n = 6$ ,  $c_u = 45$  and  $p = 0.20$ ). By contrast, two-month-old birds only marginally tracked the experimenter's gaze around the barrier ( $n = 5$ ,  $c_u = 1.33$  and  $p = 0.16$ ) but as six month olds, they did so significantly ( $n = 6$ ,  $c_u = 54$  and  $p = 0.008$ ). Two and six month olds responded to look-arounds in  $68 \pm 10\%$  and  $66 \pm 8\%$  of the cases ( $n = 5$ , 6,  $c_u = 30.5$  and  $p = 0.47$ ; figure 4), but young birds followed the experimenter's gaze *behind* the barrier about as often as *towards* the barrier ( $n = 5$ ,  $c_u = 27$  and  $p = 0.58$ ), whereas older birds clearly preferred to search behind rather than in front of the barrier ( $n = 6$ ,  $c_u = 53$  and  $p = 0.013$ ). The behaviour of the adult bird matched that of six month olds (table 1).

Although the five test sessions of a series were not conducted on consecutive days but within a 15-day period, ravens showed habituation to certain look-cues (figure 5a,b). Comparing the birds' responses between the first and the fifth trial of a series revealed a significant decrease in following the experimenter's look-ups with two-month-old birds ( $n = 6$ ,  $c_u = 54$  and  $p = 0.008$ ). A similar tendency, although not significant, was found with older birds ( $n = 7$ ,  $c_u = 63$  and  $p = 0.10$ ). By contrast, the ravens' propensity to follow the experimenter's look-arounds did not differ between the begin- and end-trials of a series, either with young birds ( $n = 5$ ,  $c_u = 25$  and  $p = 0.73$ ) or with older ones ( $n = 7$ ,  $c_u = 56$  and  $p = 0.36$ ).

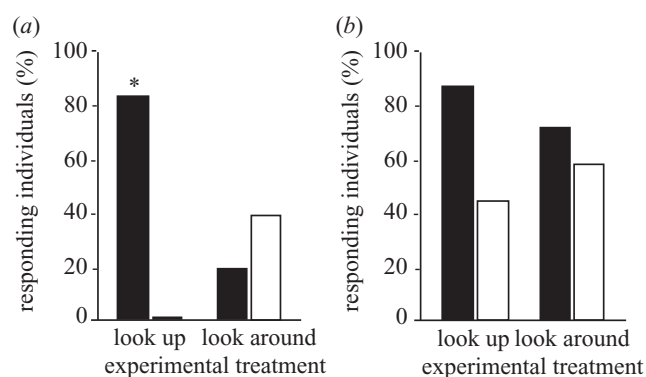
## 4. DISCUSSION

This is, to our knowledge, the first experimental demonstration that birds visually follow the gaze direction of other animate beings to distant locations and even behind obstacles, and corroborates previous findings (e.g. Hampton 1994; Watwe *et al.* 2002) that birds may be sensitive to the visual behaviour of humans.

Table 1. Number of responses of (a) two month olds, (b) six month olds, and (c) the adult during the first trial and during all trials per test series.

(Total numbers represent the sum for each individual across five trials; thus, the number possible in each cell is 5.)

			experimental treatment				experimental treatment			
			look up		control		look around		control	
			first	total	first	total	first	total	first	total
(a)	A	two months	1	1	0	0	0	0	1	1
	B	two months	1	1	0	0	1	3	0	1
	F	two months	0	1	0	0	—	—	—	—
	J	two months	1	2	0	1	0	3	0	1
	V	two months	1	3	0	1	0	1	0	0
	Z	two months	1	1	0	0	0	1	0	0
(b)	A	six months	0	1	0	0	1	3	0	0
	B	six months	1	3	1	3	0	1	0	0
	F	six months	1	3	1	4	1	2	0	1
	J	six months	1	5	0	2	1	4	0	1
	V	six months	1	2	0	1	0	2	0	0
	Z	six months	1	3	0	2	1	2	0	2
(c)	U	4 years	1	1	1	1	1	5	0	2

Figure 5. Proportion of individuals responding to E's looks in the first (filled bars) and fifth (open bars) trial of the experimental series (a) with two-month-old ravens and (b) with older ravens (six months old and adult bird). Exact Wilcoxon signed-ranks test. Asterisk denotes  $p < 0.05$ .

In response to human look-cues, ravens changed their orientation immediately and in the predicted direction. Moreover, individuals responded appropriately to the context in which the look-cues were given (Dawkins 2002). For following look-ups, they remained stationary and used the monocular lateral field of (predominantly) the left eye. The lateral head or beak position indicates that ravens were scanning for distant features (Maldonado *et al.* 1988). Owing to the nearly complete decussating of the optic nerves in birds, the lateralization in eye use points to a dominance of the right brain hemisphere, which is known to process spatial information (Güntürkün 1997). By contrast, for following look-arounds, ravens moved in the indicated direction and repeatedly alternated between eyes. Switching around between different specialized areas of retina and/or between eyes (McKenzie *et al.* 1998) is an indication that birds are trying to gain information on novel things (Dawkins 2002). The attention of young

ravens often got caught at the barrier but at about six months of age, birds repositioned themselves so that they were able to see what the experimenter was looking at.

From a cognitive point of view, the barrier results of older ravens are inconsistent with the 'low-level' model of gaze following because, unlike as young birds, they hardly paid attention to the first thing they could see (i.e. the barrier; figure 4). Instead, they geometrically followed the experimenter's gaze around the obstacle, which suggests that they were able to project a line of sight for the other person into the distance (Butterworth & Jarrett 1991; Tomasello *et al.* 1999). These findings correspond to the tactical manoeuvres that ravens show during food caching (Heinrich & Pepper 1998; Bugnyar & Kotrschal 2002b) and to other recent findings (e.g. Emery & Clayton 2001; Bond *et al.* 2003) that suggest an enormous cognitive potential of corvids in the social domain.

Although our results support the idea that ravens may understand something about the visual activities of others, the degree to which they attribute *mental* significance to the visual behaviour of others remains an open question. It has been suggested that individuals could project a line of sight without understanding that the other one is having the mental experience of 'seeing' (Butterworth & Jarrett 1991; Povinelli & Eddy 1996a; Tomasello *et al.* 1999). For instance, individuals with a natural tendency to visually co-orient with others could learn how gaze interacts with objects and obstructions and thus become quite skilful in tracking the *specific* direction of the other's gaze (i.e. to locations behind obstacles (Tomasello *et al.* 1999; Povinelli *et al.* 2000)). Nevertheless, recent findings in chimpanzees (Hare *et al.* 2000, 2001) suggest that we should remain open to the possibility that, at least in particular situations, non-human animals may understand what others can and cannot see.

From an ontogenetical point of view, our findings indicate that the two types of gaze following are differently



affected by age, with young ravens already reliably following look-ups but only older birds mastering the look-around-the-barrier task. Functionally, this difference makes sense because following look-ups may facilitate predator detection and thus would be adaptive right after fledging. Tracking the other's gaze around obstacles, by contrast, may relate mainly to the detection of food or conspecific competitors, which would not be essential as long as the birds stay with their parents. The fact that older birds produced insignificant results in following look-ups may be explained by their relatively high rates of looking up in the control condition, which suggests that they are more easily distracted by environmental cues than fledglings.

Interestingly, and unexpectedly, types of gaze following differed also in respect to habituation. Within the five trials of a test series, ravens diminished their responses to the experimenter's look-ups but not to look-arounds. This effect was clearest already in two-month-old birds, which stands in contrast to the findings in primates who start ignoring individuals that keep looking at nothing at early adulthood (Tomasello *et al.* 2001). Even more puzzling is that the five test trials with ravens were not conducted in a row but during a time period of 15 days. Possibly, this rapid habituation in following look-ups may be a result of the experimental arrangement with a human providing the look-cues. These models were lacking both behaviour that is normally associated with anti-predator scanning and consequences for not responding. Given the excellent peripheral view of birds, it is also possible that ravens have toned down the degree of their head movements in response to human look-ups rather than stopped looking at all. Further studies with additional controls are in progress.

We conclude that the gaze-follow paradigm is a useful tool to study social knowledge and visual attention in ravens. Our results suggest that the birds' gaze-follow responses may be based on different cognitive mechanisms that are differently affected by age and learning. Specifically, the ability for tracking gaze behind obstacles may provide a basis for future studies on higher-level socio-cognitive processes.

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